

# Short Communications

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## A Unique Ornament Display in Female Northern Cardinals

Jodie M. Jawor<sup>1,3</sup> and Randall Breitwisch<sup>2</sup>

**ABSTRACT.**—Females of many species of birds possess either a reduced version of male ornaments or conspicuous but hidden ornaments. No female specific ornament display has been described previously in a species with reduced or hidden female ornaments. We describe such a display in Northern Cardinals (*Cardinalis cardinalis*). The display consists of a perched female rotating her wings open to expose the red, carotenoid-pigmented underwing coverts, which are indicative of individual quality in this species. Received 19 March 2003, accepted 21 September 2003.

Birds are some of the most elaborately ornamented vertebrates. Many studies have addressed ornaments in males and their use in mate choice and intrasexual competition as indicators of condition or behavior (reviewed in Andersson 1994). The relatively few studies on female ornamentation present evidence that female ornaments can be used similarly in mate choice and intrasexual competition (reviewed in Amundsen 2000), yet no previous studies have described such a female specific display. Here we describe such a display in Northern Cardinals (*Cardinalis cardinalis*).

There are three gender patterns of ornamentation in birds. In the first, the sexes are monomorphic in ornamentation. In the second, less common pattern, females possess more elaborate ornamentation than males. In the third, the most common pattern, females possess a reduced version of the more elaborate male ornament. Lande (1980) developed the correlated response hypothesis to describe this last pattern. Under this hypothesis, female ornaments are not sexually selected but rather are the result of genome sharing between the sexes and strong selection for elaborate male ornamentation. Female ornaments are reduced in expression in response to natural selection

(e.g., to reduce nest predation; Martin and Badyaev 1996). There has been little empirical support for Lande's correlated response hypothesis. However, there is growing support for the alternative hypothesis of sexual selection maintaining female ornamentation, even when ornamentation is reduced in expression (Amundsen 2000).

Studies on sexual selection and ornamentation focus on the signal value of ornaments within the context of mate choice. In species with subdued ornament expression in females, ornaments have been linked to aspects of quality such as body size, the ability to produce nests early in the breeding season, the ability to produce many eggs, or the ability to resist disease (Burley et al. 1992, Møller 1993, Owens et al. 1994, Amundsen et al. 1997, Roulin et al. 2000, Romero-Pujante et al. 2002). In some species with subdued female ornamentation, the ornaments are visually hidden on females, presumably as a result of natural selection. For instance, the female ornament may be relatively brightly colored feathers on the ventral surface of the wing, not visible when the bird is perched, but visible in flight. We have found no previous reports of species in which females overtly display hidden ornaments to males, as we have observed in female Northern Cardinals.

Male cardinals possess red plumage over the whole body, a tall head crest, a red-orange bill, and a large black face mask. Female cardinals are tan in overall plumage color, possess a similarly tall head crest and red-orange bill, but have a smaller, less distinct face mask and have red underwing coverts. Female face mask expression, bill color, and underwing covert color all indicate aspects of individual quality (Jawor et al. in press). Male cardinals perform a variety of physical displays during courtship that draw attention to ornaments, particularly the bright red plumage of the upper breast (e.g., song-dance display, song-flight, alert display, and territorial singing dis-

<sup>1</sup> Dept. of Biology, Indiana Univ., Bloomington, IN 47405, USA.

<sup>2</sup> Dept. of Biology, Univ. of Dayton, Dayton, OH 45469-2320, USA.

<sup>3</sup> Corresponding author; e-mail: jjawor@indiana.edu

play; Lemon 1968). No female displays of ornamentation have been described previously in cardinals (see Halkin and Linville 1999).

We observed on seven occasions female cardinals displaying their underwing plumage to males during breeding seasons between 1991 and 2002. Other researchers also have observed this display in female cardinals (N. Gray, S. U. Linville, P. M. Nealen, and L. L. Wolfenbarger pers. comm.). In this display, a female perches in an accentuated upright posture facing a male, with crest erect, while holding her wings out from her body. The wings are not fully extended but rather bent at the wrist, with primaries pointed downward. The posture is reminiscent of a person holding open a jacket. The red, carotenoid-pigmented underwing coverts are presented to the male. This posture is held for  $<5$  s. There is no female vocalization accompanying the visual display. The lack of vocal announcement and short duration of the display likely are the reasons that we have observed this display so infrequently, despite hundreds of hours of focal observations of pairs of cardinals. The stance of the female is unlike that in a copulation solicitation display or a courtship feeding solicitation display (both given by female cardinals), as the female remains upright with her tail held straight down. During the lopsided display (Lemon 1968) a male cardinal may lift one wing while displaying the underside of the body. This display is quite different from the female display described here in that only one wing is lifted and partially extended away from the body, while the body is lowered and rotated about its axis (see Lemon 1968 for illustration).

All of the female displays we observed were given toward males. The members of one pair were both identified by band combinations during the display. For five of the remaining six displays observed, only one member of the pair was identified. Either the male or the female was identified by color bands during the display, and all five occurred within the boundaries of known territories. We observed the seventh display in a nearby un-banded population. We assume that the recipient of the display was the female's mate, but it is possible that this display was given to a male other than the mate.

We observed displays both early and late in

the breeding season and during mid- to late morning. We did not observe copulations or copulation attempts following the female display, although in each instance the male approached within 1 m of the displaying female. Each male was positioned for good visibility 2–7 m away from the female when the display was performed, and each male approached the displaying female either during or within 5 s of her display. Following the male's approach, the pair left the area or moved into dense vegetation. We did not observe the male giving displays of his own during the time when a female displayed, nor was any male heard to sing. The male did not appear to investigate the displaying female's plumage upon landing near her, but it is probable that the male cardinal could see the underwing plumage from several meters away. Although during our observations of this display the male did not then feed the female, one researcher (P. M. Nealen pers. comm.) has observed this sequence of events. All displays were performed 5–8 m above ground in crowns of trees with sparse leaf cover. Displays do not appear to take place near the nest, as all observed displays were well above the mean nest height in this species. We do not know the displaying females' stage of reproduction. The observed displays occurred either early in the breeding season before we had found an active nest (although one may have been present) or later in the season in cases where we had not yet found a new nest for this repeatedly nesting species.

Additional findings with cardinals suggest that the described display may communicate information on individual quality. In females, the underwing plumage is indicative of multiple aspects of quality (body size, body condition, date of first nest produced, and reproductive success; Jawor et al. in press). Also, cardinal pairs mate assortatively by ornamentation (Jawor et al. 2003); cardinal pairs possess similar bill colors, and the redness of male upper breast plumage color is positively correlated with the redness of his mate's underwing plumage color. Assortative mating is suggestive of bidirectional mate choice, and the described female display may facilitate male assessment of this condition-dependent ornament in female cardinals. This display may be integral to the formation of new pairs.

Males display their quality to females via ornamentation, and our observations suggest a reciprocal display of female quality. For established pairs, this display also may maintain pair bonds, or provide information to males on female receptivity to copulations. Cardinals nest repeatedly during the breeding season (Filliater et al. 1994) and divorces occur both within season and during winter (JM and RB unpubl. data). This situation would favor the display of individual quality at multiple times during the year, even in established pairs. Some of these suggested functions could be tested with captive cardinals in aviary experiments, although this species does not thrive in captivity (L. L. Wolfenbarger and G. E. Hill pers. comm.).

It is clear that natural selection has acted in some bird species to reduce female ornamentation from the more conspicuous male expression (Burns 1998). Less appreciated is the fact that this process has yielded hidden ornaments that are not easily assessed when a female is perching, incubating eggs, or brooding nestlings. Hidden ornaments consist of brightly colored underwing coverts, primaries, secondaries, undertail body coverts, or tail feathers that are not easily observed unless the tail or wings are spread. There are many North American species of birds in which females possess ornamental coloration that is so hidden, e.g., many warblers, Pyrrhuloxia (*Cardinalis sinuatus*), Crimson-collared Grosbeak (*Rhodothraupis celaeno*), Black-headed Grosbeak (*Pheucticus melanocephalus*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). We predict that at least some species with hidden female ornaments also possess female limited ornament displays.

Lande's (1980) correlated response hypothesis assumed that female ornaments are subdued in expression due to the influence of natural selection. We believe this assumption is warranted. However, this does not mean that subdued or hidden ornaments cannot serve as indicators of female quality under sexual selection. Hidden ornaments in female birds and, perhaps, female limited displays of these indicators of quality likely are a compromise between natural and sexual selection both acting directly on females.

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## Group Copulation Solicitation Display among Female Greater Rheas

Gustavo J. Fernández<sup>1,2</sup> and Myriam E. Mermoz<sup>1</sup>

**ABSTRACT.**—In this paper we report the copulation behavior of the Greater Rhea (*Rhea americana*), a species in which males defend a harem of females. We describe the females' behavior during 14 copulation events observed from 1995–1997 at Buenos Aires province, Argentina. During copulations, females performed a more active role than previously suggested. Moreover, on three occasions we observed that harem females performed a complex copulation solicitation display, forming a closed circle to attract the male. We hypothesize that this display could be a reliable signal to the male of the tendency of females to be inseminated and lay eggs communally. *Received 10 June 2003, accepted 15 August 2003.*

from 2 to >10 females (usually 4–6). The male copulates with each female in his harem at least once every 2–3 days, and the females lay their eggs in a single communal nest built by the male. The male performs all incubation and chick-rearing behaviors. Once the egg laying at a particular nest is completed, the females sometimes mate with other males (Astley 1907, Bruning 1974). Thus, this mating system combines harem (female defence polygyny) with sequential polyandry (Oring 1982, Jenni 1974).

The Greater Rhea (*Rhea americana*) is a precocial flightless bird that inhabits grasslands and other open habitats in the southern Neotropics. Rheas, like other ratites and some tinamous, are unusual among birds in that they combine a complex mating system with uniparental care by males. Previous studies describing the mating behavior of Greater Rheas emphasized that males perform conspicuous reproductive behavior (Raikow 1969, Bruning 1974). Female behavior, however, has been poorly described, focusing mainly on egg laying. Here we describe the mating behavior of wild Greater Rheas, including a previously unrecorded copulation solicitation display performed by the females.

Early in the breeding season (August to September) male rheas compete for and defend a group of females. Harem sizes vary

We observed Greater Rheas at General Lavalle (36° 25' S, 56° 56' W), Buenos Aires province, Argentina, during the breeding seasons of 1995–1997. The study area is a temperate grassland of the flooding Pampa (Soriano 1991). The terrain is flat, low, and marshy, with most land <10 m above sea level (see description in Fernández and Reboresda 1998). We made observations from 7:00–19:00 EST from a vehicle located 100–200 m from rhea groups.

We observed a total of 14 copulations involving seven males. All copulations occurred during morning (7:00–11:30,  $n = 6$ ) or evening (16:00–19:00,  $n = 8$ ), and copulations lasted 1–2 min. The minimum observed time between successive copulations by the same male was 20 min. For nine copulations we monitored the group before copulation solicitation took place. In six instances the male approached an isolated female of the group while she fed and he started to perform courtship displays. These involved mostly head-bobbing, in which the male moves his head vigorously up and down (Raikow 1969). The female responded to the displaying male by lowered her head and then remaining motion-

<sup>1</sup> Dep. de Ecología Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Univ. de Buenos Aires. Int. Güiraldes s/n. Pabellón 2, Ciudad Universitaria. C1428EHA Ciudad de Buenos Aires, Argentina.

<sup>2</sup> Corresponding author; e-mail: gjf@bg.fcen.uba.ar